

## 4 Regeneration dynamics

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### 4.1 INTRODUCTION

#### 4.1.1 Stability concepts

Whereas the other chapters in this book treat successional change or directional changes in the floristic composition of plant communities, this chapter deals with the regeneration dynamics of plant communities which do not appear to be experiencing successional change. Although the concepts and mechanisms discussed here apply to a variety of types of plant communities, this chapter will focus primarily on forests.

The traditional concept of the climax as formulated by Clements (1916) emphasized continued dominance of a site by the same assemblage of species as a result of the ability of climax species to establish and grow under the influences of adults of the same species. In Clementsian successional theory, a self-reproducing climax state is regarded as the culmination of progressive changes in species composition associated with the sequential arrival of propagules to a site and plant-induced environmental changes (i.e. autogenic changes) which favour the reproduction of species characteristic of later successional stages. Early criticisms of the concept emphasized the importance of allogenic changes in the physical environment (including gradual shifts in climate) that result in continued successional change so that a climax is rarely attained (Jones, 1945; Whittaker, 1953; Raup, 1957). Recent studies from a wide range of habitat types emphasize the spatial and temporal frequencies of repeated natural disturbance, such that successional development to a self-reproducing climax state is no longer viewed as the norm (White, 1979; Sousa, 1984). Nevertheless, relatively constant species compositions appear to characterize some habitats at particular spatial and temporal scales. Even in such habitats, however, repeated fine-scale disturbance is viewed as an inherent feature of the regeneration dynamics of the plant communities (Runkle, 1981; Bormann and Likens, 1979).

The degree of stability in community composition remains unresolved for many plant communities. This is due both to variation in concepts of stability and to the length of time required to assess the stability of most plant communities. As applied to plant communities, two major viewpoints on stability may be distinguished (see reviews by Holling, 1973;

Connell and Sousa, 1983). In the first, more quantitative viewpoint, constancy of numbers of individuals is emphasized. Accordingly, a stable equilibrium is defined as a particular state (e.g. population density) at which a population will remain or, if moved away from it, a state to which the population will return (Connell and Sousa, 1983). The second viewpoint emphasizes the presence or absence of species and does not require that a system remain at or return to a quantitatively defined equilibrium (Holling, 1973; Connell and Sousa, 1983). Thus, attention is shifted to how species populations in a particular habitat persist. Connell and Sousa (1983) term this qualitative viewpoint of stability *persistence*, to indicate that a species population does not become extinct during a given time period in a given area, or, if it does, it recolonizes the area within the time span required for one turnover of the population.

Given the dynamic nature of plant communities, it may not be reasonable to expect a quantitative equilibrium of population densities, particularly at small scales. Even over time periods shorter than the potential life spans of the species involved, thinning of initially dense populations is likely (see Chapter 3). Thus, qualitative persistence of species is a more appropriate criterion to apply to plant communities. Plant communities in which all the common plant species persist over time periods greater than that required for one turnover of their populations may be considered to be in *compositional equilibrium*. The concept of compositional equilibrium may be applied at a range of spatial scales. For example, for a species-rich forest in compositional equilibrium, the relative importances of species inevitably change at spatial scales corresponding to groups of a few trees (i.e.  $<25\text{ m}^2$ ) but may remain approximately constant at stand scales (thousands of square metres). Thus, scale of sampling is critical in the assessment of compositional equilibrium.

In communities in compositional equilibrium, fluctuations in the abundances of species populations may occur, but major changes in relative abundances and local extinctions are avoided. The degree of constancy in the relative abundance and dominance of different species will vary according to how narrowly the idea of compositional equilibrium is applied. For example, no variation in the relative abundances of species implies the occurrence of steady-state populations which requires a balance between establishment and mortality rates (Whittaker, 1975b). In practice, however, plant communities have been described as being in a steady state when the population age structures of the dominant species imply that they are all regenerating, even though there is usually no basis for quantitatively assessing their stabilities. This usage is essentially the same as the idea of compositional equilibrium, and is consistent with the traditional use of climax to denote relative stability of community composition.

#### 4.1.2 The patch dynamics perspective

Appreciation of spatial scale is also essential for understanding the mechanisms by which different species persist in communities at or near compositional equilibrium. At a regional or landscape scale, spatial discontinuities in plant distributions often result in a mosaic of patches which differ in composition and/or structure (Wiens, 1976; Whittaker and Levin, 1977; Pickett and Thompson, 1978; Sousa, 1984). Some of these spatial discontinuities reflect patchiness in the physical environment. However, in many cases where background physical conditions remain relatively uniform, there are marked differences in opportunities for establishment and growth of plants, which result in relatively discrete patches, sometimes consisting of individuals of similar ages (e.g. Heinselman, 1973; Oliver, 1981; Nakashizuka and Numata, 1982a; Ogden, 1985a; Oliver and Larson, 1990). This patchwork mosaic may result from the influences of disturbances on the intensity of biological interactions and resource availability. This point of view is known as the patch dynamics perspective (Pickett and Thompson, 1978). Although it has been applied effectively to a wide range of ecosystem types from intertidal marine communities to temperate grasslands (Sousa, 1979, 1984; Pickett and White, 1985; see also Chapter 2), in this chapter it will be applied mainly to the regeneration dynamics of forests.

In most plant communities of mesic habitats, where densities may potentially be great enough to render space-related resources limiting, some individuals are usually capable of dominating the site for long time periods (e.g. for at least several hundreds of years for trees). While these individuals dominate the site, environmental conditions change slowly, but eventually some of the trees die and space-related resources (e.g. light, nutrients, soil moisture) become available to other individuals. Thus, during a short time period, known as the *gap phase*, relatively rapid change occurs as new individuals attain dominance (Watt, 1923, 1947; Bray, 1956). The gap phase is characteristic of both communities near compositional equilibrium and successional communities where the replacement species do not include the formerly dominant species. Gap-phase replacement occurs in many community types (White, 1979; Sousa, 1984) but is perhaps most easily understood and best studied in mesic forests. As described many years ago by Watt (1947), fine-scale treefalls sometimes control the regeneration dynamics of mesic temperate forests, creating a mosaic of gap, building and mature phases. These are structurally distinct phases which in their sequential development constitute a forest growth cycle (Watt, 1947; Whitmore, 1975, 1982). For a forest stand in compositional equilibrium, at a particular point the canopy composition may be continually changing but over the entire stand the pattern of gap-phase replacement maintains similar relative abundances of dominant species. This viewpoint focuses attention on the gap phase

and provides a framework for the consideration of regeneration dynamics in this chapter.

#### 4.1.3 Mechanisms of species coexistence

Explanations of coexistence of plant species in communities at or near compositional equilibrium rely upon resource partitioning, life-history differentiation, or disruption of biological interactions by fine-scale disturbances, or a combination of all three (Grubb, 1977; Pickett, 1980; Aarssen, 1983; Shmida and Ellner, 1984; Silvertown and Law, 1987; Denslow, 1985; Tilman, 1988).

In explanations based on resource partitioning, natural selection is believed to result in the evolution of species with differentiated niches, so that in equilibrium communities these species coexist without competing directly. The idea that two species occupying the same niche cannot coexist indefinitely is known as Gause's hypothesis or the principle of competitive exclusion. Whittaker (1975a) described the application of this principle as follows:

- (1) If two species occupy the same niche in the same stable community, one will become extinct.
- (2) No two species observed in a stable community are direct competitors limited by the same resources; the species differ in niche in ways that reduce competition between them.
- (3) The community is a system of interacting niche-differentiated species populations that tend to complement one another, rather than directly competing, in their uses of the community's space, time, resources, and possible kinds of interactions.

For species of substantially different life-forms or patterns of seasonal development, complementarity of resource use patterns is easily envisaged (Grubb, 1977). However, for species of the same life-form and phenological behaviour in the same habitat, niche differentiation is a less attractive explanation of species coexistence. For plant species with similar modes of acquiring the same few essential resources, it is not clear how these resources can be differentially partitioned, particularly in species-rich communities (Grubb, 1977; Denslow, 1985).

Another explanation of species coexistence, known as the non-equilibrium viewpoint, suggests that disturbances truncate the process of competitive exclusion so that a compositional equilibrium with one species becoming extinct is never attained (Pickett, 1980). In this context, a *disturbance* is defined as 'a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established' (Sousa, 1984). Both biotic events, such as herbivory or pathogen attack, and abiotic events, such as fine-scale windthrow, are

frequent disturbances even in forests which appear to be at or near compositional equilibrium (Bormann and Likens, 1979; Runkle, 1982; Whitmore, 1982). According to the non-equilibrium viewpoint, most species, particularly the inferior competitors, grow to maturity when the control of the site by competitive dominants is disrupted by disturbance (Pickett, 1980). Thus, even in habitats where the background environmental conditions are uniform, periodic disturbances create spatial and temporal heterogeneity in resource availability which, in turn, permits species coexistence (see section 4.3.2).

Grubb's (1977, 1986) concept of the 'regeneration niche' as an explanation for species coexistence is consistent with both the ideas of resource partitioning and environmental heterogeneity induced by fine-scale disturbance. The *regeneration niche* of a species is 'an expression of the requirements for a high chance of success in the replacement of one mature individual by a new individual of the next generation . . .' (Grubb, 1977). According to this concept, in some communities important niche differences among coexisting species may be manifested only during the early stages of their life histories. In other words, the requirements for processes such as initiation of vegetative reproduction, propagule dispersal, germination, seedling establishment, and growth of juveniles may differ for species which have apparently undifferentiated needs as mature individuals. Changes in niche relationships as individuals grow may be the consequences of ontogenetic changes or the result of smaller individuals responding to the environment at a finer scale (Woods, 1984). The importance of micro-environmental influences on germination, establishment and early growth is also emphasized by concepts such as 'microsite mosaic' (Whittaker, 1975b) and 'safe site' (Harper, 1977). A common source of variation in these micro-environmental conditions in some communities is fine-scale disturbance.

In addition to non-equilibrium explanations of the coexistence of species which appear to have similar niches, explanations based on differences in life-history strategies have been proposed (Hutchinson, 1951; Shmida and Ellner, 1984; Silvertown and Law, 1987). Using a simple mathematical model, Shmida and Ellner (1984) predicted the coexistence of two species where one species emphasized fecundity and the other adult survivorship. Empirical support for coexistence based on differences in life-history traits comes from studies of regeneration and mortality patterns of *Picea*-*Abies* forests in the southern Appalachians and central Rockies (White *et al.*, 1985b; Veblen, 1986b). Although different species occur in the two areas, *Abies* is consistently the more abundant taxon in the seedling size class, implying greater fecundity, or at least a lower mortality rate for juveniles. In contrast, *Picea* is substantially longer lived and has a lower adult mortality rate. These differences in recruitment and mortality rates appear to contribute to the coexistence of these ecologically similar species in the same habitat.

## 4.2 RECOGNITION OF COMPOSITIONAL EQUILIBRIUM

Although it was often asserted in the older ecological literature that a particular community was in a climax state, rarely have detailed data on the populations of the constituent species been available to assess such conclusions. Since vegetation managers have traditionally accepted the idea of climax both in theory and in practice, the recognition of the climax state is of considerable practical importance. Rigorous proof of compositional equilibrium (or of steady-state populations) would require repeated measurements of a plant community over a time span equivalent to that needed for at least one turnover of all the species populations. Such observations have been made only for short-lived herbaceous plants (Connell and Sousa, 1983). In the case of forests dominated by long-lived individuals, it has not been feasible to document their species composition for time periods greater than a small fraction of the turnover period. Consequently, compositional equilibrium, as opposed to successional change, must be inferred from the past and present characteristics of the species populations. Attempts to infer the likelihood of species persistence based on demographic analysis of forest tree populations fall into three broad categories: (1) repeated censuses over multi-year periods; (2) inference of past and present demographic trends from forest structure, including dead as well as live trees; and (3) projection of future composition based on the spatial association between potential replacement individuals and canopy trees (i.e. by means of transition probabilities). Although discussed separately, these three approaches are not mutually exclusive.

### 4.2.1 Repeated censuses

There have been relatively few multi-year studies of rates of tree-seedling establishment, recruitment into succeeding age classes and direct measurement of mortality rates (e.g. Hett and Loucks, 1971, 1976; Sarukhán, 1978; Christy and Mack, 1984; Martínez-Ramos *et al.*, 1988). Generally, these have revealed a pattern of a declining mortality rate with age for the dominant tree species. Too few demographic studies of tree populations have been conducted, however, to establish whether decreasing mortality rate with age is a general pattern. Such studies have a great potential for revealing differences in regeneration niches, and if continued long enough will indicate patterns of species replacement or persistence.

A partial solution to the problem of long-term demographic observation is the inclusion of older age groups in repeated censuses. One approach is to repeatedly census different same-aged populations representing a series of stages in the development of a species' population.

Such studies can reveal the major demographic features of older cohorts (e.g. Peet and Christensen, 1980, 1987). In forests with individuals of different ages and different species, repeated observations of the populations can also reveal important differences in recruitment and mortality patterns (e.g. Christensen, 1977; Lorimer, 1981; Harcombe and Marks, 1983; Lang and Knight, 1983; Connell *et al.*, 1984; Lieberman *et al.*, 1985; Harcombe, 1986, 1987). If we can assume that the differences observed over relatively short time spans will remain consistent over the long term, repeated censuses of forest populations provide an effective means of assessing the likelihood of species persistence. This is not always a safe assumption, given the likelihood that mortality rates will change due to climatic fluctuation, site changes associated with stand development, or selective disturbances such as disease or insect attack.

#### 4.2.2 Inference from forest structure

An approach frequently used to distinguish successional trends from compositional equilibrium is based on analysis of forest stand structure. In this context, stand structure refers to the relative abundance and spatial dispersion of trees of different ages and/or sizes. In its simplest application, correspondence of the composition of seedling and sapling populations with the canopy composition has been taken as evidence of species persistence (i.e. the 'accordance' criterion of Braun, 1950). Inter-specific differences in growth rates and recruitment from juvenile stages into the canopy (e.g. Lang and Knight, 1983; Connell *et al.*, 1984) may, however, confound predictions of abundances of canopy trees based on the relative abundances of seedlings and saplings.

Stand structural analysis based on both age and size data has often been used to reconstruct details of the history of stand development, infer past mortality rates, or assess quantitative population stability. Sometimes this method has been applied without consideration of its limitations. Given the difficulty of aging large numbers of trees by counting annual rings on increment cores, size (usually diameter at breast height) is sometimes used as a substitute for age. This substitution is unavoidable for many tropical trees which usually do not form annual rings. For most temperate tree species, however, the strength of the correlation of age with diameter can be determined. In contrast to Harper's (1977) often-cited statement that the correlation of age and size in multi-aged communities 'usually turns out to be very weak', for many tree species of both the northern and southern temperate zones correlation coefficients  $>0.8$  or  $>0.9$  are often reported (Spring *et al.*, 1974; Leak, 1975; Hett and Loucks, 1976; Lorimer, 1980; Donoso *et al.*, 1984; Veblen, 1985). However, the strength of the relationship between age and diameter is highly variable, depending on species and stage of stand development, and in each case the strength of the relationship must be

investigated. Where the objective is to reconstruct the details of the history of stand development, size data alone are insufficient. However, size rather than age may be a better indicator of survival probability or reproductive capacity of trees and, hence, of their ability to contribute to the next generation of canopy trees (Harper, 1977). Size data may be sufficient, then, so long as it is only the future of the stand that is of concern.

When past mortality rates are inferred from static age structure, the individuals in successively older age classes are treated as if they were the survivors from initially equally sized cohorts. In other words, it is assumed that input into the population has remained constant over the time span represented by the oldest individuals, and that the age distribution is stationary (Caughley, 1977; Kellman, 1980). In reality, static age structure reflects past variability in both input to the population (i.e. seedling recruitment) and mortality (Harper, 1977). Nevertheless, a static age structure is often assumed to be indicative of the survivorship curves which would be observed if mortality in equal-sized cohorts was measured over time (e.g. Hett and Loucks, 1976). Given the annual variation in seed production, seed viability and seedling establishment characteristic of most tree species (Fowells, 1965; Grubb, 1977), constant input is unlikely. Consequently, tree mortality rates should not be inferred from static age structure.

Making similar assumptions, ideal age or size frequency distributions have been identified which allegedly represent stable tree populations (e.g. Liocourt, 1898; Meyer, 1952; Leak, 1964; Goff and West, 1975). When the numbers of individuals are plotted in successively larger size or older age classes, the distribution is regarded as 'balanced' if there are abundant individuals in the smallest or youngest class and progressively fewer individuals in successively larger or older classes (Meyer, 1952; Leak, 1964). Thus, as the oldest individuals die, the abundance of smaller or younger individuals allows for continued recruitment into larger or older classes so that the frequency distribution remains constant. When plotted with age or size as the horizontal axis, such a distribution is described by a smoothly declining curve which gradually approaches the horizontal axis towards greater age or size (i.e. a 'reverse J' curve in forestry terms). A negative exponential or a power function could mathematically describe the curve, depending on whether the rate of decline in successive age or size classes remains constant or decreases, respectively. The negative exponential model is  $y = a e^{bx}$ , where  $y$  is the number in any age or size class  $x$ ; 'e' is the base of the natural logarithm, and  $a$  and  $b$  are constants (Hett and Loucks, 1976; Ross *et al.*, 1982). Given a constant input of seedlings and a stationary age or size distribution, the negative exponential model implies a constant mortality rate. The power function model is  $y = ax^b$ , and given the same assumptions it implies declining mortality rates with age. Thus, these two models are

analogous to Deevey Type II and Type III survivorship curves which result from constant mortality rates and declining mortality rates with age, respectively (Pearl and Miner, 1935; Deevey, 1947).

The power function model appears to be more consistent with the observed decline in mortality rate with age in seedling cohort studies, and with the idea that juveniles are more susceptible to lethal stresses than are mature trees (Hett and Loucks, 1976; Christy and Mack, 1984). Nevertheless, either the power function or the negative exponential model may best describe the observed size or age distributions of a specific tree population (e.g. Hett and Loucks, 1976; Ross *et al.*, 1982).

While good fits of observed distributions clearly imply continuous recruitment of small or young trees into successively larger or older age classes, the same conclusion should be evident from qualitative inspection of the frequency distributions. Variation in survivorship curves of the same species occurring in different habitats suggests that such curves may be characteristic of a species in only a general way (Kellman, 1980; Butson *et al.*, 1987). Without confirmation from long-term observations, neither the negative exponential nor the power function model should be used as a strict criterion of population stability. Age-frequency distributions that are dramatically different from the negative exponential and power function models (e.g. if young individuals are scarce) are clearly indicative of population instability. However, slight departures from expected distributions should not be interpreted as evidence of population instability or of past disturbances (e.g. Jackson and Faller, 1973; Johnson and Bell, 1975).

Inclusion of data on the relative abundances of dead standing trees of different species is often useful in determining if the species composition of a stand has changed over recent decades (e.g. Ogden, 1985b; Veblen, 1986a). Identification of fallen logs on the forest floor or partially buried logs may reveal trends in species composition initiated several centuries prior to the establishment of the current canopy dominants (e.g. Henry and Swan, 1974; Oliver and Stephens, 1977; Johnson and Fryer, 1989). When growth patterns of both live and dead trees are analysed by cross-dating and measuring tree-ring widths, detailed histories of stand development are possible (Lorimer, 1985; Foster, 1988).

Although stand structural analysis without supplemental data from repeated censuses cannot be used to determine precise past recruitment and mortality rates, it can be used effectively as a time-specific method to reconstruct the major features of stand history (e.g. disturbances) and to assess the chances of species persistence (e.g. Lorimer, 1977; Nakashizuka and Numata, 1982a; Glitzenstein *et al.*, 1986; Read and Hill, 1988). Given that much of our current understanding of the regeneration dynamics of tree populations is inferred from stand structural analyses, substantial attention to the limitations of this methodology is warranted. The chances of obtaining meaningful results from stand structural analysis

can be improved by considering the following recommendations, which are aimed at relating appropriate objectives to procedures.

#### *Appropriate methods of stand structure analysis*

(i) *Collect the maximum amount of age data feasible.* Even though age determinations for large tree populations can be extremely time-consuming, such data are essential for reconstruction of the details of stand development. Also, in judging the likelihood that a species will persist at a site, it is extremely useful, if not essential, to know at least the major features of stand history (which requires age data).

(ii) *Avoid overestimating the precision of age data.* Accurate total tree ages are surprisingly difficult to obtain. The ages of trees with rotten centres are sometimes estimated by extending ring counts to the centre based on the pattern of ring-width changes in the adjacent solid portion of the tree, or by computing age-diameter regressions (e.g. Lorimer, 1980; Butson *et al.*, 1987). The proportion of the total age data represented by such estimates has to be considered when deciding on the detail of interpretation which can be justified. Other errors result from false or missing rings, inaccurate ring counts on very old individuals, and increment cores with missing centres due to either asymmetrical growth or large tree diameter relative to increment borer length (Ogden, 1985a; Duncan, 1989). Ameliorative measures such as age determination by cross-dating (Fritts, 1976), using geometric techniques to estimate the number of missing rings on cores not quite reaching the pith (Duncan, 1989), or by counting rings on cut stumps or disks (e.g. Stewart, 1986) can reduce errors, but are not always practical.

A ring count reveals the age of the tree at the level of the bole at which it is cored, not the total age (i.e. time since germination). For species which can tolerate long periods of suppression as seedlings, the difference in age between a coring height of 30 or 40 cm and total age may be several decades or more (Morris, 1948; Veblen, 1986b). To correct for this, sometimes a sample of trees is cored both at ground level to approximate total tree age and at a more convenient coring height 30–40 cm above the ground; thus, an average difference in age at ground level and at the standard coring height may be computed and added to the other trees cored only at a standard coring height (e.g. Henry and Swan, 1974). Butt rot or greater frequency of partial rings near the base of highly stressed trees, however, may make coring at ground level impractical (Fritts, 1976). Another solution is to harvest seedlings of a given height, determine their mean or modal age, and add it to the number of rings counted on cores taken at the same height. Care must be taken that the harvested seedlings grew under the same conditions (i.e. open or closed canopy) as those under which the canopy trees established.

(iii) *Where tree size accounts for a significant proportion of the data, carefully investigate the relationship between size and age.* To test the strength of this relationship, a regression of age upon diameter must be performed for a sample of trees. The size of the sample should be as large as possible, but in practice usually consists of 20–60 trees per species (e.g. Leak, 1975; Lorimer, 1980). As large a proportion of the diameter range as possible must be included by uniformly sampling all size classes (e.g. <5 cm dbh, 5–10 cm dbh, etc.). Due to variations in tree growth rates at sites of strongly different edaphic or climatic characteristics, it is logical to test the relationship of age and diameter only for samples taken from relatively uniform habitats. Samples taken over steep physical gradients usually result in weak age–diameter relationships. Even within some homogeneous stands, the relationship between tree size and age may be so weak that no inferences about regeneration patterns can be made from size data alone (e.g. Veblen, 1986a).

(iv) *Sampling and interpretation must be conducted at scales appropriate to the objective of the study.* When the objective is to describe regeneration status over a larger area (i.e. tens of thousands of hectares) large numbers of small objectively located samples are usually used (e.g. Wardle and Guest, 1977). When stand structure and regeneration status of different species vary over the area sampled, interpretation of the data pooled from numerous dispersed samples becomes problematical. Given the spatial heterogeneity of large areas and the impracticality of sampling more than a tiny fraction of large areas, any attempt to identify more than the major trends of species replacement on the basis of broad-scale surveys is inappropriate. Because the stands may have markedly different structures and disturbance histories, pooling of structural data from many different sites may also confound age–diameter relationships and obscure the circumstances in which species regenerate. When the objectives are to assess compositional equilibrium in smaller tracts of forest and reveal the circumstances in which different species regenerate, sampling at more than one scale is often effective (e.g. Lorimer, 1980). In analysing regeneration processes, it is often useful to obtain data on spatial patterns of trees, either by mapping individual trees or by contiguously locating small quadrats which will allow examination of pattern at a range of spatial scales (e.g. Williamson, 1975; Veblen *et al.*, 1981; Read and Hill, 1988; Rebertus *et al.*, 1989). For example, fine-scale clumping of a species population may indicate regeneration following small treefalls, or non-random spatial associations of species populations may indicate important influences of one species on the regeneration of another.

(v) *Incorporate autecological information into the interpretation of stand structural data.* Knowledge of the approximate potential life spans of the species studied is essential in differentiating young invasive popu-

lations of long-lived species from relatively stable populations of short-lived species. Similarly, periodicity of seed production and patterns of seed storage and germination may be reflected in the age structure of mature populations. Mechanisms and effectiveness of vegetative reproduction are often critical when comparing the likelihood of persistence of different species. For example, parental subsidy of basal sprouts for species such as *Tilia americana* may result in relatively low mortality rates of saplings compared to other species (Woods, 1984). Also, for some tree species vegetative reproduction from aerial roots and stem bases appears to compensate for lack of regeneration by new seedling establishment (Veblen *et al.*, 1981; Johnston and Lacey, 1983).

(vi) *Seek additional types of historical information on the stands studied.* For example, the relocation of historical landscape photographs can be effectively combined with quantitative analyses of stand structures (e.g. Kullman, 1986; Veblen and Lorenz, 1986, 1988). Similarly, data from land surveys sometimes allow comparisons of tree species abundances and sizes over time spans of many decades or even a century or more (e.g. Grimm, 1984).

#### 4.2.3 The transition probability approach

A third approach to the prediction of change in forest composition is the computation of a table of transition probabilities based on the spatial association of canopy trees with potential replacement individuals (for details see Chapter 6). Waggoner and Stephens (1970) and Horn (1975, 1976) proposed a model of forest stand dynamics in which succession is viewed as tree-by-tree (or, in horizontal space, cell-by-cell) replacement, and the probability of each tree being replaced by another, of the same species or by a different species, is derived from the present state of the forest. A table of transition probabilities is best constructed on the basis of remeasurements of permanent plots. Where data from permanent plots are not available, the table of transition probabilities may be constructed based on the assumption that the recruitment of canopy trees is proportional to the local abundances of subcanopy populations. Thus, the transition probabilities are computed on the basis of relative abundances of subcanopy individuals occurring beneath canopy trees (e.g. Horn, 1975; Culver, 1981) or in gaps created by the fall of different canopy species (e.g. Barden, 1981). It is assumed that the transition probability of one species replacing another species depends only on the relative abundance of subcanopy individuals of the first species occurring beneath canopy trees or in gaps created by the second species.

Although the transition probability approach has been applied effectively in numerous old-growth forests (Waggoner and Stephens, 1970; Horn, 1975, 1976; Barden, 1980, 1981; Runkle, 1981, 1984; Culver, 1981;

Ogden, 1983; Veblen, 1985; Taylor, 1990), its limitations need to be recognized. Use of the transition probability approach to predict future canopy composition is based on several assumptions, some of which are almost certainly not valid (Lippe *et al.*, 1985). Most importantly, it must be assumed that the transition probabilities remain constant over time. Due both to the effects of climate variation and changes in forest structure, transition probabilities are unlikely to remain constant. Similarly, where transition probabilities are estimated from relative abundances of saplings in the understorey, it is assumed that subcanopy individuals of different species have equal probabilities of replacing canopy trees (Horn, 1975; Usher, 1979). However, variations among species in survival and growth rates, both as seedlings and as larger subcanopy individuals, suggest that this assumption is generally not valid (Hett and Loucks, 1976; Abrell and Jackson, 1977; White *et al.*, 1985a; Veblen, 1986b). Where not already known (e.g. Fowells, 1965), major interspecific differences in growth and survival can be investigated by comparing height or radial increments (e.g. Hibbs, 1982; Kelty, 1986). Given the greater likelihood that taller individuals will reach the main canopy, predictions may alternatively be based on potential successors (i.e. the tallest subcanopy trees in each gap) instead of total abundances of saplings in gaps.

Predictions of future canopy compositions are also based on the assumption that regeneration or successional replacement is essentially a tree-by-tree replacement process resulting from small treefalls. While this assumption may be valid for some forests, in others, coarse-scale natural disturbances such as blowdown or wildfire often influence forest dynamics (e.g. Whitmore, 1974; Romme, 1982). In the absence of evidence supporting long-term site stability, the iterative use of transition probabilities over several tree generations to predict an equilibrium species composition is largely a theoretical exercise. An alternative application of the technique is to use it to test whether the present canopy composition represents compositional equilibrium (e.g. Veblen, 1985).

Many of the assumptions required in the transition probability approach are also necessary in traditional stand structure analysis, and the degree to which the transition probability approach represents a new framework for studying forest dynamics has been questioned (McIntosh, 1980). The danger of the approach is that it tends to treat forest changes as a statistical rather than an ecological process by largely ignoring interspecific differences in responses to the spatial heterogeneity of the environment associated with either canopy trees or treefall gaps (e.g. Denslow, 1980; Woods, 1984). Although explicit terms to account for variation in species' abilities to respond to treefall gaps have been suggested (e.g. Acevedo, 1981; White *et al.*, 1985a), only long-term observations can reveal the full range of variation in biological behaviour. A fundamental shortcoming lies in the implicit assumption that such a small set of variables (tree size and location) constitutes an adequate

description of complex ecological processes. The technique is, nevertheless, useful for summarizing vegetational data, discovery of major trends in species composition, and the generation of hypotheses for long-term investigation (Ogden, 1985b).

#### 4.3 THE REGENERATION NICHE AND SPECIES COEXISTENCE

##### 4.3.1 Regeneration modes

Grubb's (1977) concept of the regeneration niche emphasizes that niche differences among coexisting plant species need only be manifested during the early stages of life histories. The concept was offered as an explanation for the coexistence of species with much the same life-form, phenology and habitat range. It emphasizes the importance of fine-scale environmental heterogeneity. Disturbances may favour coexistence by contributing to environmental heterogeneity through direct modification of microsites and indirectly by altering plant influences on microsites.

A first step in characterizing a regeneration niche is to describe a species' general mode of regeneration. A species' *regeneration mode* is its regeneration behaviour in relation to disturbance. Regeneration mode refers to the spatial scale at which regeneration occurs in relation to disturbance and usually can be inferred from the age structure and spatial patterns of tree populations. A continuum of regeneration modes may be segregated arbitrarily into three types: catastrophic, gap-phase and continuous.

##### (a) The catastrophic regeneration mode

Catastrophic regeneration is the establishment of most of a local population over a relatively short period of time following a stand-devastating disturbance and sudden release of resources. Many tree species with catastrophic modes of regeneration establish massively after disturbance by wildfire, volcanic ash deposition, landslides or blowdown (White, 1979). Their populations are initially even-aged, although the age range of the cohort is highly variable according to site conditions and propagule availability (e.g. Whipple and Dix, 1979; Franklin and Hemstrom, 1981; Peet, 1981). Patch size tends to be large, often exceeding a hectare or more, and, as the patch ages, self-thinning usually results in a tendency towards less clustered tree dispersion (e.g. Ford, 1975; Kenkel, 1988). The catastrophic mode of regeneration allows many shade-intolerant tree species to coexist with shade-tolerant species that are often less effective at colonizing severely disturbed sites (e.g. Whitmore, 1974; Ashton, 1981; Veblen *et al.*, 1981; Dunn *et al.*, 1983).



*(b) The gap-phase regeneration mode*

The gap-phase mode of regeneration refers to trees attaining main canopy stature in small- to intermediate-sized canopy gaps which have resulted from the death of one tree or small groups of trees (Watt, 1947; Bray, 1956). Whereas the catastrophic regeneration mode is related mainly to exogenous disturbances, the fine-scale, gap-phase mode is a response to the endogenous treefalls which inevitably occur, both in old successional stands and in stands near compositional equilibrium (Bormann and Likens, 1979; Oliver, 1981). In many old-growth forests, regeneration in canopy gaps of this size range (c. 25–1000 m<sup>2</sup>) creates a mosaic of patches of same-aged individuals. At a stand scale this may be reflected by intense clustering of small trees and less intense clustering in old patches as the result of self-thinning (e.g. Veblen *et al.*, 1981; Nakashizuka and Numata, 1982a; Stewart, 1986; Read and Hill, 1988). Where the canopy gaps are large enough to accommodate more than one canopy tree, clumping of large trees may also be observed. When a small area (i.e. <250 m<sup>2</sup>) of a forest consisting of gap-phase species is sampled, the age distributions of individual species are likely to be sporadic (i.e. discontinuous), but at larger scales a continuously all-aged distribution should be apparent.

*(c) The continuous regeneration mode*

The continuous regeneration mode refers to attainment of maturity in the absence of a disturbance-caused canopy opening. If the main canopy is not too dense, some shade-tolerant species may sometimes grow directly into it (Spurr and Barnes, 1980; Canham, 1989). This category also includes shade-tolerant understorey trees that grow slowly to adult size but rarely reach the upper part of the forest canopy. These understorey specialists are most common in tropical rainforests and apparently do not require gaps for either germination or growth to reproductive maturity (Whitmore, 1974; Denslow, 1980). This category also includes canopy tree species which reach ~~and~~ main canopy by establishing epiphytically and then growing <sup>is</sup> vines through even dense canopies in some southern temperate forests (Veblen *et al.*, 1981; Wardle, 1983). In contrast to the other two regeneration modes, the availability of the resources required for regeneration of these species is much more continuous. Compared to the other two modes, however, the continuous mode of regeneration appears to be rare.

A particular regeneration mode may be characteristic of a species in only a general way, and may vary with forest type or stage of stand development (Veblen, 1989). For example, *Pinus contorta* in the central Rocky Mountains is well known as a species which regenerates mainly after wildfire (Stahelin, 1943; Daubenmire, 1943). Its catastrophic regeneration mode generally maintains its abundance in subalpine

habitats where its range overlaps with the more shade-tolerant *Picea engelmannii* and *Abies lasiocarpa*, which, in the absence of fire, successional replace it (Peet, 1981; Veblen, 1986a). However, in less favourable habitats, such as on particularly nutrient-poor soils and xeric sites, the species which otherwise would successional replace it may be unable to grow. In such habitats, and also in Sierran subalpine forests in California, *Pinus contorta* regenerates in old-growth stands long unaffected by wildfire in a gap-phase mode, beneath small- to intermediate-sized treefall gaps (Whipple and Dix, 1979; Peet, 1981; Despain, 1983; Parker, 1986).

## 4.3.2 Regeneration in treefall gaps

As trees grow taller and develop more massive crowns, they become more susceptible to windthrow. As a tree ages, other factors also contribute to the increasing risk of windthrow, including decreasing physiological efficiency and the weakening effects of disease and insect attack (Brokaw, 1985b; Runkle, 1985; Worrall and Harrington, 1988). In some tropical rainforests heavy loads of epiphytes and lianas may also contribute to treefalls (Strong, 1977; Putz, 1984). For a given forest, the rate of treefalls results from the interaction of internal factors like tree architecture, stratification and health, with external factors such as type and intensity of precipitation and wind speeds and durations. Thus, although the characteristics of treefalls are not totally controlled by the plants themselves, small treefalls approximate the concept of endogenous disturbance more closely than any other type of common disturbance (Bormann and Likens, 1979).

Even in the absence of treefalls, there is substantial heterogeneity beneath a 'closed' forest canopy in terms of composition, height, thickness and foliage density, which may have important influences on understorey composition and subsequent responses to treefalls (Veblen *et al.*, 1979b; Lieberman *et al.*, 1989). In fact, the dichotomy between gap and non-gap sites in a forest is arbitrary, given the continuum of variation in light levels within a forest (Canham, 1989; Lieberman *et al.*, 1989). Nevertheless, the dichotomy between gap and non-gap sites is a useful point of departure for understanding regeneration dynamics. There are three general mechanisms by which treefalls temporarily increase the availability of resources for plant growth. The first is simply the decrease in rate of uptake and use of resources (such as solar radiation, soil moisture and soil nutrients) due to the loss of biomass, both in the canopy and the undergrowth (Vitousek and Denslow, 1986; Denslow *et al.*, 1990). The second is the decay and mineralization of nutrients previously held in organic matter. The latter results from both decomposition of the fallen trees and from higher rates of decomposition of soil organic matter associated with increased insolation and temperature at the soil surface



(Bormann and Likens, 1979). The third is simply the exposure of bare mineral soil where a thick litter layer previously may have impeded seedling establishment.

There are two general patterns of vegetation response to the transient pulses of resources associated with treefalls (Marks, 1974; Canham and Marks, 1985). The reorganization pattern involves accelerated growth of individuals already established at the time of the treefall. Examples include lateral encroachment of branches and roots from surrounding trees, vegetative spread of understorey species, epicormic branching of undamaged trees, sprouting and root suckering of damaged individuals, and release of previously suppressed seedlings and saplings (i.e. 'advance regeneration' in forestry). The new establishment pattern includes both establishment from dormant seeds already in place at the time of the treefall as well as from propagules dispersed to the site following the treefall. It also includes the establishment of tree seedlings that originate as canopy epiphytes and subsequently establish in gaps as trees fall in some tropical rainforests (Lawton and Putz, 1988). Within the reorganization and new establishment patterns, more detailed differences in responses to treefall gaps further differentiate the regeneration niches of tree species. The following treefall gap characteristics appear to be significant in the divergence of regeneration niches, and, thereby, may contribute to species coexistence in forests that are at or near compositional equilibrium.

#### (a) Gap size, shape and orientation

Gap size is related both to tree sizes and the manner in which they fall. As expected, for gaps created by the fall of a single tree, gap area is positively correlated with tree size (Brokaw, 1982). The largest gaps result from multiple treefalls, when a large canopy tree knocks down its neighbours in a domino fashion. Relatively small gaps are created when a tree dies in a standing position and gradually collapses downwards. Limb falls generally create the smallest gaps. Small gaps have a greater perimeter-to-area ratio than larger gaps, which may significantly influence the pattern of vegetation response. In smaller gaps the relative importance of encroachment of lateral growth of branches and roots from the surrounding trees will be greater (Runkle, 1985). Similarly, in smaller gaps and in more irregularly shaped gaps, the greater number of nearby mature trees per unit gap area will favour more rapid propagule recruitment.

The microclimate of gaps varies as a function of latitude, gap size, and shape and orientation in relation to the height of the surrounding trees (Geiger, 1965; Lee, 1978; Poulson and Platt, 1989; Canham *et al.*, 1990). In tropical forests maximum initial light intensities should be greater and should occur closer to the centre of the gap than in temperate forests

(Poulson and Platt, 1989). As gap size increases, so does intensity and duration of solar radiation, mean soil and air temperature, and temperature ranges; conversely, humidity decreases with size (Denslow, 1980; Runkle, 1985; Brokaw, 1985b; Moore and Vankat, 1986; Collins and Pickett, 1987). Gap shape and orientation also influence gap microclimate. For example, long narrow gaps allow less insolation at the ground surface than circular gaps of the same size (Tomanek, 1960 in Runkle, 1985). The shape and orientation of the gap with respect to the heights of surrounding trees also influence the amount of direct solar radiation. For example, in some temperate forest gaps there is a stronger relationship between sapling abundance and direct solar radiation during the growing season than between sapling abundance and either gap area or total solar radiation (Veblen *et al.*, 1979a). Similarly, in an eastern deciduous forest in North America, gap orientation has been shown to influence light levels and ingrowth by surrounding trees (Poulson and Platt, 1989).

Given the strong influence of gap size on dispersal probabilities and gap microclimate, it is not surprising that many tree species are specialized according to the size of the gap in which they are likely to regenerate (Denslow, 1980, 1987; Runkle, 1982; Brokaw, 1985a, 1987; Brokaw and Scheiner, 1989; Whitmore, 1989). The mechanisms which determine the success of different tree species in gaps of varying sizes may involve differences in germination, vegetative reproduction or seedling establishment. For species such as *Prunus pensylvanica* in the northeast United States, and many tree species in neotropical rainforests, treefalls trigger massive germination of viable seeds stored in the soil (Marks, 1974; Vázquez-Yanes and Smith, 1982; Young *et al.*, 1987; Raich and Khoon, 1990). Experimental studies have shown that the germination triggers involve the higher temperatures, light levels, or ratio of red/far-red light typical of gaps (Bazzaz and Pickett, 1980; Canham and Marks, 1985). In addition to being hormone-mediated responses to direct damage to trees, branching from epicormic buds or sprouting from stumps to roots may also be responses to environmental cues associated with treefall gap environments (Zimmerman and Brown, 1971). Seedlings of many tree species are differentiated by their response to amounts of solar radiation. For example, generally there is a direct relationship between the growth rate of a tree species in large gaps and the minimum gap size required for net growth of seedlings (Grime, 1966; Marks, 1975).

#### (b) Time and periodicity of gap creation

The time of the year during which treefalls are most frequent varies greatly from one forest to another (Brokaw, 1985b). Since in most habitats the production of propagules is seasonal for the majority of tree species, time of gap creation may be an important influence on the availability of

propagules to colonize gaps (Brokaw, 1982; Canham and Marks, 1985). The seasonality of gap creation may even be a selective force on the timing of dispersal or germination of gap-phase species (Brokaw, 1982). Propagule availability is less influenced by seasonal variation in the creation of gaps when dormant propagules are stored in the soil (e.g. *Prunus pensylvanica*) or on parent trees (e.g. *Eucalyptus regnans*) (Marks, 1974; Ashton, 1976).

The periodicity of treefall gaps may have major influences on the species composition of a forest (Denslow, 1980; Runkle, 1985). Inspection of growth ring patterns of canopy trees in temperate forests often reveals multiple releases and suppressions, implying several episodes of gap creation and closure (Henry and Swan, 1974; Oliver and Stephens, 1977; Nakashizuka and Numata, 1982a; Runkle, 1985; Veblen, 1985, 1986b; Canham, 1990). Often before a canopy gap can be closed, the fall of surrounding trees will expand the gap and subject the gap occupants to further environmental changes (Hartshorn, 1978; Runkle, 1984; Foster and Reiners, 1986). This pattern of periodic gap expansion may allow gap-phase species to reach the canopy in gaps which initially may have been too small. Many shade-tolerant tree species are capable of multiple episodes of release and suppression in response to treefall dynamics (Runkle, 1985; Veblen, 1985; Runkle and Yetter, 1987). Thus, after equal time periods, a site affected by a single large treefall may be dominated by shade-intolerant canopy trees, whereas a site affected by multiple small treefall gaps totalling the same area would be expected to be dominated by more shade-tolerant canopy trees.

Multiple treefall episodes affecting the same site confound the concept of *gap turnover rate*, which is the mean time between successive creations of gap areas at any one point in the forest (Brokaw, 1985b). The most reliable estimates of gap turnover rate are based on annual observations in permanent plots over a period of time (e.g. Hartshorn, 1978; Brokaw, 1982; Foster and Brokaw, 1982; Uhl, 1982). In these studies overlapping gaps may be taken into account. Less reliable estimates are derived from size and age frequencies of presently recognizable gaps, sometimes taking into account rates of gap closure by lateral encroachment and upward growth (e.g. Runkle, 1982; Nakashizuka, 1984; Veblen, 1985; Taylor, 1990). Barden (1989) showed that slight differences in definitions and sampling methods (e.g. defined entry height into the canopy, minimum diameter of trees capable of creating gaps, and transect samples versus full enumerations of gaps) may result in large differences in estimated turnover rates. Thus, estimates of gap turnover rate reflect both real differences among forests as well as variations in methodology.

For both tropical and temperate mesic forests with disturbance regimes dominated by small- to intermediate-sized gaps, mean gap turnover rates are c. 100 years; the range is from c. 50 to 575 years (Runkle, 1982; Nakashizuka, 1984; Brokaw, 1985b; Veblen, 1985; Foster and Reiners,

1986). Two observations reconcile these relatively short mean turnover times with average tree longevities of 300–600 years for many of the dominants of temperate forests (Runkle, 1985). First, multiple gap episodes occur at some sites before a first gap is created at other sites, resulting in a large range of possible turnover times for any given site. Second, many potentially dominant trees survive gap creation as sub-canopy trees a hundred or more years old. Despite the difficulties of making reliable measurements, turnover rates of large areas of forests dominated by frequent fine-scale disturbance do not appear to differ greatly from those dominated by coarse-scale exogenous disturbances (Runkle, 1985). Thus, the frequencies of gaps of different sizes may be of more significance in explaining community composition than mean turnover time (e.g. Brokaw, 1985a, 1987).

### (c) Influences of gap-creating species

Canopy trees of different species sometimes influence the species composition of the nearby understorey vegetation through their effects on the establishment, growth and mortality of herbs and seedlings of woody plants (e.g. Veblen *et al.*, 1979b; Hicks, 1980; Woods and Whittaker, 1981; McGuire and Forman, 1983; Beatty, 1984; Augspurger, 1983a). If future development of vegetation in a gap depends on advance regeneration, or if the effects of the canopy tree persist after its death, then there may be a non-random spatial association of the species of the former canopy tree and the replacement species. These effects may be manifested as reciprocal replacement (i.e. alternation of species), which has been reported for numerous types of northern temperate forest (Fox, 1977; Woods, 1979, 1984; Runkle, 1984).

The causes of differential success of saplings and seedlings under certain canopy species or in gaps created by certain species are not clear. Microsite differences beneath canopy species may result from variations in the quantity and quality of litter, which, in turn, may affect availability of soil nutrients or result in allelopathic interactions (e.g. Zinke, 1962; Tubbs, 1973; Gauch and Stone, 1979; Beatty and Sholes, 1988; Boettcher and Kalisz, 1990). Canopy trees may also differentially alter understorey light levels or soil moisture (e.g. Anderson, 1964; Browne and Bourn, 1973). Microsite differences may result from interspecific variation in the pattern of canopy tree death. For example, species which tend to die standing create different microsites than those that are more prone to wind-snap or uprooting (Falinski, 1978; Putz *et al.*, 1983; Beatty and Stone, 1986). In addition to seedling responses to direct modification of the microsite by the canopy tree, canopy influence may be mediated through indirect biological interactions. For example, canopy species may differentially influence the abundance and size of understorey plants which, in turn, may affect the establishment and growth of tree seedlings

(e.g. Veblen *et al.*, 1979b; MaGuire and Forman, 1983). Also, Connell (1971) and Janzen (1970) suggested that in tropical rainforests the presence of host-specific pests and pathogens near canopy trees could decrease growth and survival of conspecific seedlings. According to the Janzen–Connell hypothesis for coexistence of tropical tree species, herbivores and pathogens will be concentrated near food plants and will cause high mortality in a cluster of offspring near their parents. Despite some negative tests (e.g. Hubbell, 1979; Connell *et al.*, 1984), several studies in tropical rainforests support the idea (e.g. Augspurger, 1983a,b; Clark and Clark, 1984).

(d) *Within-gap environmental heterogeneity*

Divergence of regeneration niches may involve differential abilities to establish and grow in the spatially heterogeneous environment of a tree-fall gap. In an idealized gap created by the fall of a single canopy tree in a dense forest, the fallen tree trunk forms the axis of a dumbbell-shaped area of damage to adjacent canopy trees and undergrowth (Orians, 1982; Brokaw, 1985b). Environmental conditions along the bole of the fallen tree are likely to be different from those near the crown, and both may be different from conditions near the upturned root mass. For example, the root zone usually includes a pit of exposed mineral soil and a mound of upturned soil and decaying roots which differ in their physical and chemical properties from each other and from the crown and trunk zones (e.g. Beatty, 1984; Vitousek and Denslow, 1986; Beatty and Scholes, 1988; Schaetzel *et al.*, 1989). The smothering effect and massive input of nutrients from the decaying foliage of the crown may create microsites different from those associated with the trunk or root zone. In most gaps, the fall of subcanopy trees and breakage of the canopy tree create a complex pattern of microrelief and scattered debris beneath irregularly shaped canopy openings. The aspects of the gap environment most likely to differentially influence the vegetation response include the nature of the surface, presence of understorey plants and presence of other kinds of organisms.

Within a gap there is a mosaic of microsites which may affect seed lodgement, germination or survival. For example, tip up mounds often have a significantly different floristic composition than pits or the undisturbed forest floor (Beatty, 1984; Nakashizuka, 1989; Peterson *et al.*, 1990). Plant growth rates may also be different in different microhabitats within a gap (Uhl *et al.*, 1988). A 'nurse-log' syndrome is characteristic of many temperate rainforest species, such as those of northwestern North America (Franklin and Dyrness, 1973), New Zealand (Odgen, 1971) and southern Chile (Veblen *et al.*, 1981). In these instances, survival of seedlings is better on fallen logs and stumps than on the litter-covered forest floor. Growth to maturity following germination on logs requires

establishment of firm root anchorage in the soil before the supporting log decays. Observation of large trees with logs still beneath them indicates that at least some seedlings survive and attain main canopy stature. Greater seedling survival on logs appears to result from the negative influences of tree leaf litter on seedling emergence and survival on the forest floor, and from reduced competition from herbs and mosses (Sydes and Grime, 1981; Christy and Mack, 1984; Harmon and Franklin, 1989), or it may involve differential availability of nutrients or moisture (Graham and Cromack, 1982). Use of logs as rodent trails may also influence dispersal and seedling survival (Falinski, 1978). The differential species composition of mounds versus pits is well known and may be explained by either contrasting soil properties, differential dispersal, and/or greater herbivory at one type of microsite (Hutnik, 1952; Falinski, 1978; Thompson, 1980; Putz, 1983; Beatty, 1984).

Occupation of treefall gaps by understorey species is often a critical influence on the rate and composition of canopy species regeneration (e.g. Ehrenfeld, 1980; Brokaw, 1983). The falling tree damages or kills some understorey plants by bending, breaking, uprooting or burial, but in many cases a large part of the undergrowth remains intact. Initially, the density of understorey species depends on their density prior to the treefall, so that falls occurring in patches of dense canopy and low light levels may result in gaps of greater resource availability for gap colonists. Sometimes the relative importance of understorey and canopy species' response to gaps is related to gap size, with larger gaps favouring understorey species (e.g. Huenneke 1983; Veblen 1985). A dramatic example of inhibition of the response of canopy species to treefall gaps involves the proliferation of bamboos in gaps in many tropical and temperate forests (Oshima, 1961; Shidei, 1974; Whitmore, 1975; Veblen, 1982; Nakashizuka and Numata, 1982b; Taylor and Zisheng, 1988). The interference from bamboos in gaps not only varies with their initial abundances beneath the forest canopy, but also with gap size, influences of herbivores on the bamboo, and timing of gap creation with respect to synchronous flowering and death of bamboo clones (Veblen, 1982, 1985; Nakashizuka and Numata, 1982b).

Relatively little is known about the spatial heterogeneity of herbivores, pathogens, seed predators and animal vectors of dispersal within gaps. However, variation in the presence of these organisms is potentially important to the recruitment and survival of tree seedlings. For example, foraging of ants which may nest in or near logs is important in seed predation and dispersal (Ashton, 1979; Thompson, 1980). Similarly, seeds of fleshy fruits are sometimes left on fallen logs in the faeces of birds and mammals, and fleshy fruits may have a higher probability of being eaten in gaps than beneath a closed canopy (Thompson and Willson, 1978; Thompson, 1980). On the other hand, in some forests new gaps provide few resources to birds and due to exposure to predators are

dangerous perching sites; thus, animal-mediated seedfall in gaps may be lower (Brokaw, 1986; Schupp *et al.*, 1989). Large upturned tree butts and relatively impenetrable masses of large logs sometimes provide safe sites for seedlings of species which otherwise are destroyed by large, ground-dwelling herbivores (Falinski, 1978). Micro-organisms associated with roots or with leaf litter may have a deleterious effect on tree seedlings (e.g. Florence, 1965) so that the depth of soil disturbance may sometimes be critical to seedling establishment and survival.

#### 4.4 REGENERATION DYNAMICS AND LANDSCAPE PATTERNS

The emphasis in this chapter has been on regeneration processes occurring at the scale of gaps produced by the fall of individual trees or small groups of trees. Regeneration processes at these fine scales result in forest stands which consist of a mosaic of subunits (typically less than 1000 m<sup>2</sup>) of varying structure and composition. Regeneration processes may also occur at the scale of an entire stand affecting areas of several hectares to many square kilometres. Thus, consideration of disturbance events which affect large areas is essential not only to an understanding of broad-scale vegetation patterns, but also to species coexistence at a regional scale (Forman and Godron, 1981; Urban *et al.*, 1987; Ricklefs, 1987).

In many forested landscapes a self-reproducing climax or compositional equilibrium may only rarely be attained and, if so, often at only relatively large spatial scales. Coarse-scale exogenous disturbances such as fire, mass movements, insect outbreaks and extensive blowdown are widespread and sometimes frequent enough to have a controlling influence on forest structure and composition at a landscape scale (e.g. Heinzelman, 1973; Whitmore, 1974; Veblen and Ashton, 1978; Garwood *et al.*, 1979; Ashton, 1981; Romme, 1982; Canham and Loucks, 1984; Johnson and Fryer, 1987; Knight, 1987; Veblen *et al.*, 1991). Thus, at a stand scale, attainment of compositional equilibrium may be prevented by frequent exogenous disturbance. In landscapes dominated by coarse-scale disturbances, populations of early successional tree species may periodically become locally extinct. If common tree species persist at similar levels of abundance over large areas, however, the landscape as a whole may be in a state of *global equilibrium*, or 'shifting-mosaic steady-state' (Bormann and Likens, 1979). Assessment of compositional equilibrium, then, requires sampling of forest composition over an entire landscape. This usually involves a combination of ground sampling and mapping of vegetation units from aerial photographs (e.g. Heinzelman, 1973; Johnson and Fryer, 1987).

At a landscape scale, the proportions of different stand types (differentiated by composition and/or structure) may be related to the nature and history of disturbances which have affected the landscape. The

concept of *disturbance regime* is a means of organizing spatial and temporal information about a range of disturbances affecting a particular landscape (Sousa, 1984; White and Pickett, 1985; see also Chapter 3). The key descriptors of a disturbance regime are: (1) spatial distribution of occurrence, particularly in relation to environmental gradients; (2) frequency of occurrence; (3) size of the area disturbed; (4) mean return interval (i.e. the inverse of frequency); (5) predictability; (6) rotation period (the time required to disturb an area equivalent in size to the study area); (7) magnitude of the disturbance measured either directly as the intensity of the disturbing agent or indirectly as the impact on the vegetation (i.e. severity); and (8) the synergistic interactions of different kinds of disturbances. Available descriptions of disturbance regimes, however, are only partial and usually deal exclusively with a single type of disturbance such as endogenous treefall (e.g. Runkle, 1982) or fire (e.g. Romme, 1982). To understand the role of disturbance in creating broad landscape patterns, the full range of disturbances affecting a particular landscape must be considered (e.g. Harmon *et al.*, 1983).

#### SUMMARY

1. A plant species may be termed persistent if its population does not become extinct during a given time period in a given area, or, if it does, it recolonizes the area within the time span required for one turnover of its population. Plant communities in which all the common plant species are persistent may be judged to be in compositional equilibrium.
2. A critical consideration in the assessment of compositional equilibrium is the spatial scale at which it is investigated. In a vegetation mosaic consisting of small patches of different species composition, individual patches are often not in compositional equilibrium, even though equilibrium may exist at the spatial scale of the entire mosaic.
3. The patch dynamics perspective emphasizes the importance of periodic disturbance in creating opportunities for establishment of new individuals or growth of previously suppressed individuals by releasing the resources utilized by the former dominants of the site. Investigation at a wide range of spatial scales of the temporal and spatial characteristics of disturbances and plant population responses to disturbances is essential to an understanding of the regeneration dynamics and vegetation patterns in any landscape.
4. Recognition of compositional equilibrium in contrast to successional trends is methodologically difficult for long-lived organisms such as trees. The surest method, but also the least practical, requires repeated censuses over multi-year periods. Faster but less certain methods include stand structural analysis and computation of transition probabilities. Both methods must be applied with great caution

due to the unlikelihood of obtaining all the data required (e.g. many trees cannot be precisely aged) and the difficulty, without long-term studies, of verifying assumptions underlying these techniques.

5. In forest stands at or near compositional equilibrium, species persistence often involves a combination of resource partitioning and non-equilibrium mechanisms of coexistence. For many tree species, differences in resource needs and mode of acquiring resources may be manifested only during the early stages in their life histories, as emphasized by the regeneration niche concept. Fine-scale disturbance in the form of treefalls, however, also favours coexistence by truncating processes of competitive exclusion and by contributing to the spatial and temporal heterogeneity of resource availability.
6. The regeneration niches of tree species may be differentiated in relation to the heterogeneity of resource availability associated with: (1) gap size, shape and orientation; (2) seasonality and periodicity of gap creation; (3) the micro-environmental influences of the canopy tree which previously occupied the gap; (4) the nature of substrates within gaps; (5) abundance and composition of gap-occupying understorey plants; or (6) presence of animals and micro-organisms within gaps. While differences in regeneration niches are often critical to the coexistence of tree species, differences among mature trees in their influences on microsites and in their mortality patterns also contribute significantly to their coexistence.

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## REFERENCES

- Aarssen, L. W. (1983) Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *Amer. Nat.*, **122**, 707–31.
- Abrell, D. B. and Jackson, M. T. (1977) A decade of change in an old-growth beech-maple forest in Indiana. *Amer. Mid. Nat.*, **98**, 22–32.
- Acevedo, M. F. (1981) On Horn's Markovian model of forest dynamics with particular reference to tropical forests. *Theor. Pop. Biol.*, **19**, 230–50.
- Anderson, M. C. (1964) Light relations of terrestrial plant communities and their measurement. *Biol. Rev.*, **39**, 425–86.
- Ashton, D. H. (1976) Even-aged stands of *Eucalyptus regnans* F. Muell. in central Victoria. *Austral. J. Bot.*, **24**, 397–414.
- Ashton, D. H. (1979) Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in Victoria. *Austral. J. Ecol.*, **4**, 265–77.
- Ashton, D. H. (1981) Fire in tall open-forests (wet sclerophyll forests), in *Fire in the Australian Biota* (eds A. M. Gill and I. R. Noble), SCOPE, Canberra, pp. 339–66.
- Augspurger, C. K. (1983a) Offspring recruitment around tropical trees: Changes in cohort distance with time. *Oikos*, **40**, 189–96.
- Augspurger, C. K. (1983b) Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *J. Ecol.*, **71**, 759–71.
- Baker, W. L. (1989) Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. *Ecology*, **70**, 23–35.
- Barden, L. S. (1980) Tree replacement in a cove hardwood forest in the southern Appalachians. *Oikos*, **35**, 16–19.
- Barden, L. S. (1981) Forest development in canopy gaps of a diverse hardwood forest of southern Appalachian Mountains. *Oikos*, **37**, 205–9.
- Barden, L. S. (1989) Repeatability in forest gap research: studies in the Great Smoky Mountains. *Ecology*, **70**, 558–9.
- Bazzaz, F. A. and Pickett, S. T. A. (1980) Physiological ecology of tropical succession: A comparative review. *Ann. Rev. Ecol. System.*, **11**, 287–310.
- Beatty, S. W. (1984) Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology*, **65**, 1406–19.
- Beatty, S. W. and Sholes, O. D. (1988) Leaf litter effect on plant species composition of deciduous forest treefall pits. *Canad. J. For. Res.*, **18**, 553–9.
- Beatty, S. W. and Stone, E. L. (1986) The variety of soil microsites created by treefalls. *Canad. J. For. Res.*, **16**, 539–48.
- Boettcher, S. E. and Kalisz, P. J. (1990) Single-tree influence on soil properties in the mountains of eastern Kentucky. *Ecology*, **71**, 1365–72.
- Bormann, F. H. and Likens, G. E. (1979) *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York.
- Braun, E. L. (1950) *Deciduous Forests of Eastern North America*, McGraw-Hill, New York.
- Bray, J. R. (1956) Gap phase replacement in a maple-basswood forest. *Ecology*, **37**, 598–600.
- Brokaw, N. V. L. (1982) Treefalls: frequency, timing, and consequences, in *The Ecology of a Tropical Forest: Seasonal Rhythms and Longer-term Changes* (eds E. G. Leigh, Jr. A. S. Rand and D. W. Windsor), Smithsonian Institution Press, Washington, D.C., pp. 101–108.
- Brokaw, N. V. L. (1983) Groundlayer dominance and apparent inhibition of tree regeneration by *Acchmea magdalenae* (Bromeliaceae) in a tropical forest. *Trop. Ecol.*, **24**, 194–200.
- Brokaw, N. V. L. (1985a) Gap-phase regeneration in a tropical forest. *Ecology*, **66**, 682–7.
- Brokaw, N. V. L. (1985b) Treefalls, regrowth, and community structure in tropical forests, in *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett and P. S. White), Academic Press, New York, pp. 53–69.
- Brokaw, N. V. L. (1986) Seed dispersal, gap colonization, and the case of



- Cecropia insignis*, in *Frugivory and Seed Dispersal* (eds A. Estrada and T. H. Gleming), Junk, Dordrecht, pp. 323–31.
- Brokaw, N. V. L. (1987) Gap-phase regeneration of three pioneer tree species in a tropical forest. *J. Ecol.*, **75**, 9–19.
- Brokaw, N. V. L. and Scheiner, S. M. (1989) Species composition in gaps and structure of a tropical forest. *Ecology*, **70**, 538–41.
- Browne, J. H. Jr and Bourn, T. G. (1973) Patterns of soil moisture depletion in a mixed oak stand. *Forest Sci.*, **19**, 23–30.
- Butson, R. G., Knowles, P. and Farmer, R. E. Jr (1987) Age and size structure of marginal, disjunct populations of *Pinus resinosa*. *J. Ecol.*, **75**, 685–92.
- Canham, C. D. (1989) Different responses to gaps among shade-tolerant tree species. *Ecology*, **69**, 548–50.
- Canham, C. D. (1990) Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bull. Torrey Bot. Club*, **117**, 1–7.
- Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A. and White, P. S. (1990) Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canad. J. For. Res.*, **20**, 620–31.
- Canham, C. D. and Loucks, O. L. (1984) Catastrophic windthrow in the pre-settlement forests of Wisconsin. *Ecology*, **65**, 803–9.
- Canham, C. D. and Marks, P. L. (1985) The response of woody plants to disturbance: patterns of establishment and growth, in *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett and P. S. White), Academic Press, New York, pp. 197–216.
- Caughley, G. (1977) *Analysis of Vertebrate Populations*, Wiley, Chichester.
- Christensen, J. L. (1977) Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. *Amer. Mid. Nat.*, **97**, 176–88.
- Christy, E. J. and Mack, R. N. (1984) Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *J. Ecol.*, **72**, 75–91.
- Clark, D. A. and Clark, D. B. (1984) Spacing dynamics of a tropical rainforest tree: evaluation of the Janzen-Connell model. *Amer. Nat.*, **124**, 769–88.
- Clements, F. E. (1916) *Plant Succession: An Analysis of the Development of Vegetation*, Carnegie Institution of Washington, Publ. 242.
- Collins, B. S. and Pickett, S. T. A. (1987) Influence of canopy opening on the environment and herb layer in a northern hardwoods forest. *Vegetatio*, **70**, 3–10.
- Connell, J. H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees, in *Dynamics of Populations* (eds P. J. den Boer and G. Gradwell), Proc. Adv. Study Inst., Oosterbeek, 1970. Center for Agric. Publishing and Documentation, Wageningen, The Netherlands, pp. 298–312.
- Connell, J. H. and Sousa, W. P. (1983) On the evidence needed to judge ecological stability or persistence. *Amer. Nat.*, **121**, 789–824.
- Connell, J. H., Tracey, J. G. and Webb, L. J. (1984) Compensatory recruitment, growth, and mortality as factors maintaining forest tree diversity. *Ecol. Monogr.*, **54**, 141–64.
- Culver, D. C. (1981) On using Horn's Markov succession model. *Amer. Nat.*, **117**, 572–4.
- Daubenmire, R. F. (1943) Vegetational zonation in the Rocky Mountains. *Bot. Rev.*, **9**, 325–93.
- Deevey, E. S. Jr (1947) Life tables for natural populations of animals. *Quart. Rev. Biol.*, **22**, 383–14.
- de Liocourt, F. (1898) De l'aménagement des sapinières. *Bull. Soc. Forestière Franche-Comte*, **4**, 396–409.
- Denslow, J. S. (1980) Gap partitioning among tropical rain forest trees. *Biotropica* (Suppl.), **12**, 47–55.
- Denslow, J. S. (1985) Disturbance-mediated coexistence of species, in *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett and P. S. White), Academic Press, New York, pp. 307–23.
- Denslow, J. S. (1987) Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. System.*, **18**, 431–51.
- Denslow, J. S., Shultz, J. C., Vitousek, P. M. and Strain, B. R. (1990) Growth responses of tropical shrubs to treefall gap environments. *Ecology*, **71**, 165–79.
- Despain, D. G. (1983) Nonpyrogenous climax lodgepole pine communities in Yellowstone National Park. *Ecology*, **64**, 231–4.
- Donoso, C., Grez, R., Escobar, B. and Real, P. (1984) Estructura y dinámica de bosques del tipo forestal siempreverde en un sector de Chiloé insular. *Bosque*, **5**, 82–104.
- Duncan, R. P. (1989) An evaluation of errors in tree age estimates based on increment cores in kahikatea (*Dacrydium dacrydioides*). *New Zealand Nat. Sci.*, **16**, 31–7.
- Dunn, C. P., Guntenspergen, G. R. and Dorney, J. R. (1983) Catastrophic wind disturbance in an old-growth hemlock-hardwood forest, Wisconsin. *Canad. J. Bot.*, **61**, 211–17.
- Ehrenfeld, J. G. (1980) Understory response to canopy gaps of varying size in a mature oak forest. *Bull. Torrey Bot. Club*, **107** (2), 29–41.
- Falinski, J. G. (1978) Uprooted trees, their distribution and influence in the primeval forest biotope. *Vegetatio*, **38**, 175–83.
- Florence, R. G. (1965) Decline of old-growth redwood forests in relation to some soil microbiological processes. *Ecology*, **46**, 52–64.
- Ford, E. D. (1975) Competition and stand structure in some even-aged plant monocultures. *J. Ecology*, **63**, 311–33.
- Forman, R. T. T. and Godron, M. (1981) Patches and structural components for a landscape ecology. *BioScience*, **31**, 733–40.
- Foster, D. R. (1988) Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, south-western New Hampshire, U.S.A. *J. Ecol.*, **76**, 105–34.
- Foster, J. R. and Reiners, W. A. (1986) Size distribution and expansion of canopy gaps in a northern Appalachian spruce fir forest. *Vegetatio*, **68**, 109–14.
- Foster, R. B. and Brokaw, N. V. L. (1982) Structure and history of the vegetation of Barro Colorado Island, in *The Ecology of a Neotropical Forest: Seasonal Rhythms and Longer-term Changes* (eds E. G. Leigh Jr, A. S. Rand and D. M. Windsor), Smithsonian Institution Press, Washington, D.C., pp. 67–81.
- Fowells, H. A. (1965) *Silvics of Forest Trees of the United States*, US Government Printing Office, Washington, D.C.
- Fox, J. F. (1977) Alternation and coexistence of tree species. *Amer. Nat.*, **111**, 69–89.
- Franklin, J. F. and Dyrness, C. T. (1973) *Natural Vegetation of Oregon and Washington*, USDA Forest Service General Technical Report, PNW-8.

- Franklin, J. F. and Hemstrom, M. F. (1981) Aspects of succession in the coniferous forests of the Pacific Northwest, in *Forest Succession: Concepts and Applications* (eds D. C. West, H. H. Shugart and D. B. Botkin), Springer-Verlag, New York, pp. 212–29.
- Fritts, H. C. (1976) *Tree Rings and Climate*, Academic Press, New York.
- Garwood, N. C., Janos, D. P. and Brokaw, N. (1979) Earthquake-caused landslides: A major disturbance to tropical forests. *Science*, **205**, 997–9.
- Gauch, H. G. and Stone, E. L. (1979) Vegetation and soil pattern in a mesophytic forest at Ithaca, New York. *Amer. Mid. Nat.*, **102**, 332–45.
- Geiger, R. (1965) *The Climate Near the Ground*, Harvard Univ. Press, Cambridge.
- Glitzenstein, J. S., Harcombe, P. A. and Streng, D. R. (1986) Disturbance, succession, and maintenance of species diversity in an east Texas forest. *Ecol. Monogr.*, **56**, 243–58.
- Goff, F. G. and West, D. (1975) Canopy-understory interaction effects on forest population structure. *Forest Sci.*, **21**, 98–108.
- Graham, R. L. and Cromack, K., Jr (1982) Mass. nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Canad. J. For. Res.*, **12**, 511–21.
- Grime, J. P. (1966) Shade avoidance and shade tolerance in flowering plants, in *Light as an Ecological Factor* (eds R. Bainbridge, G. C. Evans and O. Rackham), Blackwell, London, pp. 187–207.
- Grimm, E. C. (1984) Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecol. Monogr.*, **54**, 291–311.
- Grubb, P. J. (1977) The maintenance of species richness in plant communities. The importance of regeneration niche. *Biol. Rev.*, **52**, 107–45.
- Grubb, P. J. (1986) Problems posed by sparse and patchily distributed species in species-rich plant communities, in *Community Ecology* (eds J. Diamond and T. J. Case), Harper and Row, New York, pp. 207–25.
- Harcombe, P. A. (1986) Stand development in a 130-year-old spruce-hemlock forest based on age structure and 50 years of mortality data. *Forest Ecol. Mgmt.*, **14**, 41–58.
- Harcombe, P. A. (1987) Tree life tables, *BioScience*, **37**, 557–68.
- Harcombe, P. A. and Marks, P. L. (1983) Five years of tree death in *Fagus-Magnolia* forest, southeast Texas (USA). *Oecologia*, **57**, 49–54.
- Harmon, M. E., Bratton, S. P. and White, P. S. (1983) Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. *Vegetatio*, **55**, 129–39.
- Harmon, M. E. and Franklin, J. F. (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology*, **70**, 48–59.
- Harper, J. L. (1977) *Population Biology of Plants*, Academic Press, London.
- Hartshorn, G. S. (1978) Tree falls and tropical forest dynamics, in *Tropical Trees as Living Systems* (eds P. B. Tomlinson and M. H. Zimmerman), Cambridge Univ. Press, Cambridge, Mass., pp. 617–38.
- Heinselman, M. L. (1973) Fire in the virgin forests of the Boundary Water Canoe Area, Minnesota. *Quat. Res.*, **3**, 329–82.
- Henry, J. D. and Swan, J. M. A. (1974) Reconstructing forest history from live and dead plant material – an approach to the study of forest succession in southwest New Hampshire. *Ecology*, **55**, 772–83.
- Hett, J. M. and Loucks, O. L. (1971) Sugar maple (*Acer saccharum* Marsh.) seedling mortality. *J. Ecol.*, **59**, 507–20.
- Hett, J. M. and Loucks, O. L. (1976) Age structure models of balsam fir and eastern hemlock. *J. Ecol.*, **64**, 1029–44.
- Hibbs, D. E. (1982) Gap dynamics in a hemlock-hardwood forest. *Canad. J. For. Res.*, **12**, 522–7.
- Hicks, D. J. (1980) Intrastand distribution patterns of southern Appalachian cove forest herbaceous species. *Amer. Mid. Nat.*, **104**, 209–23.
- Holling, C. S. (1973) Resilience and stability of ecological systems. *Ann. Rev. Ecol. System.*, **4**, 1–23.
- Horn, H. S. (1975) Markovian processes of forest succession, in *Ecology and Evolution of Communities* (eds M. L. Cody and J. M. Diamond), Harvard Univ. Press, Cambridge, Mass., pp. 196–211.
- Horn, H. S. (1976) Succession, in *Theoretical Ecology: Principles and Applications* (ed. R. M. May), Saunders, Philadelphia, pp. 187–204.
- Hubbell, S. P. (1979) Tree dispersion, abundance and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.
- Huenneke, L. F. (1983) Understory response to gaps caused by the death of *Ulmus americana* in central New York. *Bull. Torrey Bot. Club*, **110**, 170–5.
- Hutnik, R. J. (1952) Reproduction on windfalls in a northern hardwood stand. *J. Forestry*, **50**, 693–4.
- Hutchinson, G. E. (1951) Copepodology for the ornithologist. *Ecology*, **32**, 571–7.
- Jackson, M. T. and Faller, A. (1973) Structural analysis and dynamics of the plant communities of Wizard Island, Crater Lake National Park. *Ecol. Monogr.*, **43**, 441–61.
- Janzen, D. H. (1970) Herbivores and the number of tree species in tropical forests. *Amer. Nat.*, **104**, 501–27.
- Johnson, E. A. and Fryer, G. (1987) Historical vegetation change in the Kananaskis Valley, Canadian Rockies. *Canad. J. Bot.*, **65**, 853–8.
- Johnson, E. A. and Fryer, G. (1989) Population dynamics in lodgepole pine–Engelmann spruce forests. *Ecology*, **70**, 1335–45.
- Johnson, F. L. and Bell, D. T. (1975) Size-class structure of three streamside forests. *Amer. J. Bot.*, **62**, 81–5.
- Johnston, R. D. and Lacey, C. J. (1983) Multi-stemmed trees in rainforest. *Austral. J. Bot.*, **31**, 189–95.
- Jones, E. W. (1945) The structure and reproduction of the virgin forest of the north temperate zone. *New Phytol.*, **44**, 130–48.
- Kellman, M. C. (1980) *Plant Geography*, 2nd edn. St Martin's, New York.
- Kelty, M. T. (1986) Development patterns in two hemlock-hardwood stands in southern New England. *Canad. J. For. Res.*, **16**, 885–91.
- Kenkel, N. C. (1988) Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology*, **69**, 1017–24.
- Knight, D. H. (1987) Parasites, lightning, and the vegetation mosaic in wilderness landscapes, in *Landscape Heterogeneity and Disturbance* (ed. M. G. Turner), Springer-Verlag, New York, pp. 59–83.
- Kullman, L. (1986) Recent tree-limit history of *Picea abies* in the southern Swedish Scandes. *Canad. J. For. Res.*, **16**, 761–71.
- Lang, G. E. and Knight, D. H. (1983) Tree growth, mortality, recruitment, and



- canopy gap formation during a 10-year period in a tropical moist forest. *Ecology*, **64**, 1075–80.
- Lawton, R. O. and Putz, F. E. (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology*, **69**, 764–77.
- Leak, W. B. (1964) An expression of diameter distribution for unbalanced, uneven-aged stands and forests. *Forest Sci.*, **10**, 39–50.
- Leak, W. B. (1975) Age distribution in virgin red spruce and northern hardwoods. *Ecology*, **56**, 1451–4.
- Lee, R. (1978) *Forest Microclimatology*, Columbia Univ. Press, New York.
- Lieberman, D., Lieberman, M., Peralta, R. and Hartshorn, G. S. (1985) Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.*, **73**, 915–24.
- Lieberman, M., Lieberman, D. and Peralta, R. (1989) Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology*, **70**, 550–2.
- Lippe, E., de Smidt, J. T. and Glenn-Lewin, D. C. (1985) Markov models and succession: a test from a heathland in the Netherlands. *J. Ecol.*, **73**, 775–91.
- Lorimer, C. G. (1977) The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology*, **58**, 139–48.
- Lorimer, C. G. (1980) Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology*, **61**, 1169–84.
- Lorimer, C. G. (1981) Survival and growth of understory trees in oak forests of the Hudson Highlands, New York. *Canad. J. For. Res.*, **11**, 689–95.
- Lorimer, C. G. (1985) Methodological considerations in the analysis of forest disturbance history. *Canad. J. For. Res.*, **15**, 200–13.
- MaGuire, D. A. and Forman, R. T. T. (1983) Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. *Ecology*, **64**, 1367–80.
- Marks, P. L. (1974) The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.*, **44**, 73–88.
- Marks, P. L. (1975) On the relation between extension growth and successional status of deciduous trees of the northeastern United States. *Bull. Torrey Bot. Club*, **102**, 172–7.
- Martínez-Ramos, M., Sarukhan, J. and Pinero, D. (1988) The demography of tropical trees in the context of forest gap dynamics, in *Plant Population Ecology* (eds D. J. Davy, M. J. Hutchings and A. R. Watkinson), Blackwell, Oxford, pp. 293–313.
- McIntosh, R. P. (1980) The relationship between succession and the recovery process in ecosystems, in *The Recovery Process in Damaged Ecosystems* (ed. J. Cairns), Ann Arbor Science Publication, Ann Arbor, Mich, pp. 11–62.
- Meyer, H. A. (1952) Structure, growth, and drain in balanced uneven-aged forests. *J. Forestry*, **50**, 85–92.
- Moore, M. R. and Vankat, J. L. (1986) Responses of the herb layer to the gap dynamics of a mature beech maple forest. *Amer. Mid. Nat.*, **115**, 336–47.
- Morris, R. F. (1948) How old is a balsam tree? *Forestry Chron.*, **24**, 106–10.
- Nakashizuka, T. (1984) Regeneration process of climax beech (*Fagus crenata* Blume) forests. IV. Gap formation. *Japan. J. Ecol.*, **33**, 409–18.
- Nakashizuka, T. (1989) Role of uprooting in composition and dynamics of an old-growth forest in Japan. *Ecology*, **70**, 1273–8.
- Nakashizuka, T. and Numata, M. (1982a) Regeneration process of climax beech forests. I. Structure of a beech forest with the undergrowth of Sasa. *Japan. J. Ecol.*, **32**, 57–67.
- Nakashizuka, T. and Numata, M. (1982b) Regeneration process of climax beech forests. II. Structure of a forest under the influences of grazing. *Japan. J. Ecol.*, **32**, 473–82.
- Ogden, J. (1971) Studies on the vegetation of Mount Colenso New Zealand. 2. The population dynamics of Red Beech. *Proc. New Zealand Ecol. Soc.*, **18**, 66–75.
- Ogden, J. (1983) Community matrix model predictions of future forest composition at Russell State Forest. *New Zealand J. Ecol.*, **6**, 71–7.
- Ogden, J. (1985a) An introduction to plant demography with special reference to New Zealand trees. *New Zealand J. Bot.*, **23**, 751–72.
- Ogden, J. (1985b) Past, present and future: Studies on the population dynamics of some long-lived trees, in *Studies on Plant Demography: A Festschrift for John L. Harper* (ed. J. White), Academic Press, London, pp. 3–16.
- Oliver, C. D. (1981) Forest development in North America following major disturbances. *Forest Ecol. Mgmt*, **3**, 153–68.
- Oliver, C. D. and Larson, B. C. (1990) *Forest Stand Dynamics*, McGraw-Hill, New York.
- Oliver, C. D. and Stephens, E. P. (1977) Reconstruction of a mixed-species forest in central New England. *Ecology*, **32**, 84–103.
- Orians, G. H. (1982) The influence of tree-falls in tropical forests on tree species richness. *Trop. Ecol.*, **23**, 255–79.
- Oshima, Y. (1961) Ecological studies of Sasa communities. I. Productive structure of some of the Sasa communities in Japan. *Bot. Mag. Tokyo*, **74**, 199–210.
- Parker, A. J. (1986) Persistence of lodgepole pine forests in the central Sierra Nevada. *Ecology*, **67**, 1560–7.
- Pearl, R. and Miner, J. R. (1935) Experimental studies on the duration of life. XIV. The comparative mortality of certain lower organisms. *Quart. Rev. Biol.*, **10**, 67–79.
- Peet, R. K. (1981) Forest vegetation of the Colorado Front Range: Composition and dynamics. *Vegetatio*, **45**, 3–75.
- Peet, R. K. and Christensen, N. L. (1980) Succession: A population process. *Vegetatio*, **43**, 131–40.
- Peet, R. K. and Christensen, N. L. (1987) Competition and tree death. *BioScience*, **37**, 586–95.
- Peterson, C. J., Carson, W. P., McCarthy, B. C. and Pickett, S. T. A. (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos*, **58**, 39–46.
- Pickett, S. T. A. (1980) Non-equilibrium coexistence of plants. *Bull. Torrey Bot. Club*, **107**, 238–48.
- Pickett, S. T. A. and Thompson, J. N. (1978) Patch dynamics and the design of nature reserves. *Biol. Conserv.*, **13**, 27–37.
- Pickett, S. T. A. and White, P. S. (eds) (1985) *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, New York.
- Poulson, T. L. and Platt, W. J. (1989) Gap light regimes influence canopy tree diversity. *Ecology*, **70**, 553–5.
- Putz, F. E. (1983) Treefall pits and mounds, buried seeds, and the importance of

- soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology*, **64**, 1069–74.
- Putz, F. E. (1984) How trees avoid and shed lianas. *Biotropica*, **16**, 19–23.
- Putz, F. E., Coley, P. D., Lu, K. and Montalvo, A. (1983) Uprooting and snapping of trees: Structural determinants and ecological consequences. *Canad. J. For. Res.*, **13**, 1011–20.
- Raich, J. W. and Khoon, G. W. (1990) Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *J. Trop. Ecol.*, **6**, 203–17.
- Raup, H. H. (1957) Vegetational adjustment to the instability of site. *Proc. Paper 6th Tech. Meeting Int. Union Conserv. Naturalist Res. (Edinburgh)*, pp. 36–48.
- Read, J. and Hill, R. S. (1988) The dynamics of some rainforest associations in Tasmania. *J. Ecol.*, **76**, 558–84.
- Rebertus, A. J., Williamson, G. B. and Moser, E. B. (1989) Fire-induced changes in *Quercus laevis* spatial pattern in Florida Sandhills. *J. Ecol.*, **77**, 638–50.
- Ricklefs, R. E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–71.
- Romme, W. H. (1982) Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecol. Monogr.*, **52**, 199–221.
- Ross, M. S., Sharik, T. L. and Smith, D. W. (1982) Age-structure relationships of tree species in an Appalachian oak forest in southwest Virginia. *Bull. Torrey Bot. Club*, **109**, 287–98.
- Runkle, J. R. (1981) Gap regeneration in some old-growth forests of the eastern United States. *Ecology*, **62**, 1041–51.
- Runkle, J. R. (1982) Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, **63**, 1533–46.
- Runkle, J. R. (1984) Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarctic Ecol.*, **7**, 157–64.
- Runkle, J. R. (1985) Disturbance regimes in temperate forests, in *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett and P. S. White), Academic Press, New York, pp. 17–33.
- Runkle, J. R. and Yetter, T. C. (1987) Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology*, **68**, 417–24.
- Sarukhan, J. (1978) Studies on the demography of tropical trees, in *Tropical Trees and Living Systems* (eds P. B. Tomlinson and M. H. Zimmerman), Cambridge Univ. Press, Cambridge, Mass., pp. 163–84.
- Schaetzl, R. J., Burns, S. F., Johnson, D. L. and Small, T. W. (1989) Tree uprooting: review of impacts on forest ecology. *Vegetatio*, **79**, 165–76.
- Schupp, E. W., Howe, H. F., Augspurger, C. K. and Levey, D. J. (1989) Arrival and survival in tropical treefall gaps. *Ecology*, **70**, 562–4.
- Shidei, T. (1974) Forest vegetation zones, in *The Flora and Vegetation of Japan* (ed. M. Numata), Elsevier, Amsterdam, pp. 87–124.
- Shmida, A. and Ellner, S. (1984) Coexistence of plant species with similar niches. *Vegetatio*, **58**, 29–55.
- Silvertown, J. and Law, R. (1987) Do plants need niches? Some recent developments in plant community ecology. *Trends Ecol. Evol.*, **2**, 24–6.
- Sousa, W. P. (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, **60**, 1225–39.
- Sousa, W. P. (1984) The role of disturbance in natural communities. *Ann. Rev. Ecol. System.*, **15**, 353–91.
- Spring, P. E., Brewer, M. L., Brown, J. R. and Fanning, M. E. (1974) Population ecology of loblolly pine *Pinus taeda* in an old field community. *Oikos*, **25**, 1–6.
- Spurr, S. H. and Barnes, B. V. (1980) *Forest Ecology*, 3rd edn, Wiley, New York.
- Stahelin, R. (1943) Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. *Ecology*, **24**, 19–30.
- Stewart, G. H. (1986) Population dynamics of a montane conifer forest, western Cascade Range, Oregon, U.S.A. *Ecology*, **67**, 534–44.
- Strong, D. R. (1977) Epiphyte loads, treefalls, and perennial forest disruption: A mechanism for maintaining higher tree species richness in the tropics without animals. *J. Biogeog.*, **4**, 215–18.
- Sydes, C. and Grime, J. P. (1981) Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. *J. Ecol.*, **69**, 237–48.
- Taylor, A. H. (1990) Disturbance and persistence of sitka spruce (*Picea sitchensis* (Bong) Carr.) in coastal forests of the Pacific Northwest. *J. Biogeog.*, **17**, 47–58.
- Taylor, A. H. and Zisheng, Q. (1988) Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong Natural Reserve, Sichuan, China. *J. Ecol.*, **76**, 1204–18.
- Thompson, J. N. (1980) Treefalls and colonization patterns of temperate forest herbs. *Amer. Mid. Nat.*, **104**, 176–84.
- Thompson, J. N. and Willson, M. F. (1978) Disturbance and the dispersal of fleshy fruits. *Science*, **200**, 1161–3.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*, Princeton Univ. Press, Princeton, New Jersey.
- Tomanek, J. (1960) Mikroklimatische Verhältnisse in Lochhiebe, in *Verh. Ganzstaatle Bioklimatol. Konf.*, 1958, pp. 297–313.
- Tubbs, C. H. (1973) Allelopathic relationships between yellow birch and sugar maple seedlings. *Forest Sci.*, **19**, 139–45.
- Uhl, C. (1982) Tree dynamics in a species rich tierra firme forest in Amazonia, Venezuela. *Acta Cientifica Venezolana*, **33**, 72–7.
- Uhl, C., Clark, K., Dezzio, N. and Maquirino, P. (1988) Vegetation dynamics in Amazonian treefall gaps. *Ecology*, **69**, 751–63.
- Urban, D. L., O'Neill, R. V. and Shugart, H. H., Jr (1987) Landscape ecology. *BioScience*, **37**, 119–27.
- Usher, M. B. (1979) Markovian approaches to ecological succession. *J. Animal Ecol.*, **48**, 413–26.
- Vázquez-Yanes, C. and Smith, H. (1982) Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper aurinum* and its ecological significance. *New Phytol.*, **92**, 477–85.
- Veblen, T. T. (1982) Growth patterns of *Chusquea* bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. *Bull. Torrey Bot. Club*, **109**, 474–87.
- Veblen, T. T. (1985) Forest development in tree-fall gaps in the temperate rain forests of Chile. *Nat. Geog. Res.*, **1**, 162–83.
- Veblen, T. T. (1986a) Age and size structure of subalpine forests in the Colorado Front Range. *Bull. Torrey Bot. Club*, **113**, 225–40.

- Veblen, T. T. (1986b) Treefalls and the coexistence of conifers in subalpine forests of the central Rockies. *Ecology*, **67**, 644–9.
- Veblen, T. T. (1989) Tree regeneration responses to gaps along a transandean gradient. *Ecology*, **70**, 541–3.
- Veblen, T. T. and Ashton, D. H. (1978) Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio*, **36**, 149–67.
- Veblen, T. T., Ashton, D. H. and Schlegel, F. M. (1979a) Tree regeneration strategies in a lowland *Nothofagus*-dominated forest in south-central Chile. *J. Biogeog.*, **6**, 329–40.
- Veblen, T. T., Veblen, A. T. and Schlegel, F. M. (1979b) Understory patterns in mixed evergreen-deciduous *Nothofagus* forests in Chile. *J. Ecol.*, **67**, 809–23.
- Veblen, T. T., Donoso Z. C., Schlegel, F. M. and Escobar R. B. (1981) Forest dynamics in south-central Chile. *J. Biogeog.*, **8**, 211–47.
- Veblen, T. T., Hadley, K. S., Reid, M. S. and Rebertus, A. J. (1991) The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology*, **72**, 213–31.
- Veblen, T. T. and Lorenz, D. C. (1986) Anthropogenic disturbance and recovery patterns in montane forests. Colorado Front Range. *Phys. Geog.*, **7**, 1–24.
- Veblen, T. T. and Lorenz, D. C. (1988) Recent vegetation changes along the forest/steppe ecotone of northern Patagonia. *Ann. Ass. Amer. Geog.*, **78**, 93–111.
- Vitousek, P. M. and Denslow, J. S. (1986) Nitrogen and phosphorous availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.*, **74**, 1167–78.
- Waggoner, P. E. and Stephens, G. R. (1970) Transition probabilities for a forest. *Nature*, **225**, 1160–1.
- Wardle, J. and Guest, R. (1977) Forests of the Waitaki and Lake Hawaea catchments. *New Zealand J. For. Sci.*, **7**, 44–67.
- Wardle, P. (1983) Temperate broad-leaved evergreen forests of New Zealand, in *Temperate Broad-Leaved Forests* (ed. J. D. Ovington), Elsevier, Amsterdam, pp. 33–71.
- Watt, A. S. (1923) On the ecology of British beechwoods with special reference to their regeneration. Part I. The causes of failure of natural regeneration of the beech (*Fagus sylvatica* L.). *J. Ecol.*, **11**, 1–48.
- Watt, A. S. (1947) Pattern and process in the plant community. *J. Ecol.*, **35**, 1–22.
- Whipple, S. A. and Dix, R. L. (1979) Age structure and successional dynamics of a Colorado subalpine forest. *Amer. Mid. Nat.*, **101**, 142–58.
- White, P. S. (1979) Pattern, process, and natural disturbance in vegetation. *Bot. Rev.*, **45**, 229–99.
- White, P. S., Mackenzie, M. D. and Busing, R. T. (1985a) Natural disturbance and gap phase dynamics in southern Appalachian spruce–fir forests. *Canad. J. For. Res.*, **15**, 233–40.
- White, P. S., Mackenzie, M. D. and Busing, R. T. (1985b) A critique on overstory/understory comparisons based on transition probability analysis of an old growth spruce–fir stand in the Appalachians. *Vegetatio*, **64**, 37–45.
- White, P. S. and Pickett, S. T. A. (1985) Natural disturbance and patch dynamics: An introduction, in *The Ecology of Natural Disturbance and Patch Dynamics* (eds S. T. A. Pickett and P. S. White), Academic Press, New York, pp. 3–13.
- Whitmore, T. C. (1974) *Change with Time and the Role of Cyclones in Tropical Rain Forest of Kolombangara, Solomon Islands*, Commonwealth Forestry Institute Paper, No. 46, University of Oxford.
- Whitmore, T. C. (1975) *Tropical Rain Forests of the Far East*, Oxford Univ. Press, London.
- Whitmore, T. C. (1982) On pattern and process in forests, in *The Plant Community as a Working Mechanism* (ed. E. I. Newman), Blackwell, Oxford, pp. 45–59.
- Whitmore, T. C. (1989) Canopy gaps and the two major groups of forest trees. *Ecology*, **70**, 536–8.
- Whittaker, R. H. (1953) A consideration of climax theory: The climax as a population and pattern. *Ecol. Monogr.*, **23**, 41–8.
- Whittaker, R. H. (1975a) *Communities and Ecosystems*, 2nd edn, MacMillan, New York.
- Whittaker, R. H. (1976b) The design and stability of plant communities, in *Unifying Concepts in Ecology* (eds W. H. van Dobben and R. H. Lowe-McConnell), Junk, The Hague, pp. 169–81.
- Whittaker, R. H. and Levin, S. A. (1977) The role of mosaic phenomena in natural communities. *Theor. Pop. Biol.*, **12**, 117–39.
- Wiens, J. A. (1976) Population responses to patchy environments. *Ann. Rev. Ecol. System.*, **7**, 81–120.
- Williamson, G. B. (1975) Pattern and seral composition in an old-growth beech-maple forest. *Ecology*, **56**, 727–31.
- Woods, K. D. (1979) Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos*, **33**, 31–9.
- Woods, K. D. (1984) Patterns of tree replacement: Canopy effects on understory pattern in hemlock–northern hardwood forests. *Vegetatio*, **56**, 87–107.
- Woods, K. D. and Whittaker, R. H. (1981) Canopy–understory interaction and the internal dynamics of mature hardwood and hemlock–hardwood forests, in *Forest Succession: Concepts and Application* (eds D. C. West, H. H. Shugart and D. B. Botkin), Springer-Verlag, New York, pp. 305–23.
- Worrall, J. J. and Harrington, T. C. (1988) Etiology of canopy gaps in spruce–fir forests at Crawford Notch, New Hampshire. *Canad. J. For. Res.*, **18**, 1463–9.
- Young, K. R., Ewel, J. J. and Brown, B. J. (1987) Seed dynamics during forest succession in Costa Rica. *Vegetatio*, **71**, 157–73.
- Zimmerman, M. H. and Brown, C. L. (1971) *Trees: Structure and Function*, Springer, New York.
- Zinke, P. J. (1962) The pattern of influence of individual forest trees on soil properties. *Ecology*, **43**, 130–3.